# Functional Properties Shared By Populations of Neighboring Neurons within the Thalamocortical Pathway

By

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## INTRODUCTION

Most of the visual information from the retina has to pass through a small thalamic structure called the lateral geniculate nucleus (LGN) to reach the cerebral cortex (in humans, each LGN is barely larger than an almond ~ 120 mm$^3$). The axons of these thalamic neurons are very numerous (~ 1 million in humans) and are topographically organized. That is, neighboring regions within the LGN project to neighboring regions within the primary visual cortex. The topographic organization of the thalamocortical pathway provides the basis for a detailed representation of visual space within the primary visual cortex, usually known as the retinotopic map.

The retinotopic map is only one of the multiple maps that are represented within the primary visual cortex. Other maps include representations of line orientation, ocular dominance, motion direction and spatial frequency (for review, see Chklovskii and Koulakov 2004). Hubel and Wiesel were the first to demonstrate the functional organization of orientation columns within the cat visual cortex by doing careful electrophysiological experiments (Hubel and Wiesel 1962). A decade later, with the use of a glucose analog, 2-deoxyglucose, the same authors provided an anatomical picture of the orientation columns (Hubel et al. 1978) and another decade had to pass before it became possible to visualize these orientation columns in the living cortex with optical imaging (Grinvald et al. 1986). The use of optical imaging has been exploited since then to study the organization of the multiple maps that are represented in the brain (Bartfeld and Grinvald 1992; Basole et al. 2003; Blasdel 1992a, b; Crair et al. 1997; Everson et al. 1998; Hubener et al. 1997; Obermayer et al. 1992; Swindale 2000; Weliky et al. 1996; White et al. 2001; Xu et al. 2005; Yu et al. 2005).

The existence of all these maps motivated two highly productive lines of research. Computational neuroscientists became interested in understanding how the multiple maps could be fit within a two-dimensional sheet of primary visual cortex, which is not larger than a credit card [~25 cm$^2$ in humans, (Bartfeld and Grinvald 1992; Basole et al. 2003; Blasdel 1992b; Crair et al. 1997; Everson et al. 1998; Hubener et al. 1997; Obermayer et al. 1992; Swindale 2000; Weliky et al. 1996; White et al. 2001; Xu et al. 2005; Yu et al. 2005)]. On the other hand, a large number of experimentalists began to combine neuroanatomy, imaging and electrophysiological techniques to reveal the arrangements of horizontal connections (Bosking et al. 1997; Gilbert and Wiesel 1989; Kisvarday et al. 1997; Malach et al. 1993; Yoshioka et al. 1996), feedback connections (Shmuel et al. 2005; Stettler et al. 2002) and vertical intracortical connections (Mooser et al. 2004) within orientation and ocular dominance maps.

These studies led to an increasingly detailed understanding on the contribution from different types of intracortical connections (horizontal, feedback and vertical connections) to the representation of multiple cortical maps. Paradoxically, we still have a very poor understanding about the contribution of the thalamic afferents to these maps, even if cortical retinotopic maps have been historically attributed to the topographic organization of the thalamocortical pathway. In fact, although we know that neighboring regions of the LGN project to neighboring regions in the cortex, we do not know how this topographic organization is arranged at the submillimeter scale. For example, we do not have precise measurements of the scatter in receptive field position from the multiple geniculate afferents that converge at each cortical point nor we have a good

understanding on how the scatter in receptive field position relates to the functional organization of orientation maps (Chapman et al. 1991).

The main goal of this dissertation was to fill these gaps in our understanding of the functional arrangement of geniculate afferents both at the level of the thalamus and the primary visual cortex. The first aim measured the response properties shared by neighboring cells within the thalamus with traditional visual stimuli. The second aim investigated how the shared properties of neighboring neurons change with the stimulus conditions. The third aim investigated the response properties shared by geniculate afferents that converge at the same cortical domain. Finally, the fourth aim measured the response properties of geniculate cells under natural scene stimulation.

The cat visual system is an excellent model to address these specific aims. There is an extensive anatomical and physiological database on the cat thalamocortical pathway that can be used for the interpretation of the results (for review, see Gilbert 1983; Orban 1984; Sherman and Guillery 2001). Moreover, the cat visual system shares basic organizing principles with the primate and human visual systems (e.g. parallel and separate thalamocortical pathways projecting at the middle layers of the cortex). Cats have also coarser retinotopic maps than primates and humans, making the retinotopic alignment of thalamic and cortical electrodes a feasible task.

## SUMMARY OF EXPERIMENTAL STUDIES

**Aim 1. Response properties of neighboring LGN neurons (Appendices I & IV)**

We live surrounded by a large variety of visual stimuli that differ in size, position, shape, color, speed of movement, and other attributes. The mammalian visual system has developed parallel pathways to analyze each of these attributes independently. The idea of 'parallel pathways', was clearly enunciated by Semir Zeki a few decades ago (Zeki 1976), and since then it has been become one of the major tenets of Visual Neuroscience (Lee 1993, 1996; Lee et al. 1996; Lennie 1980; Rodieck 1979; Sherman 1985; Sherman and Spear 1982; Stone et al. 1979). In the cat, there are two main pathways, X and Y, which differ in morphological and physiological features. On average, Y geniculate cells have larger receptive field sizes and respond faster to visual stimuli than X geniculate cells at the same eccentricity (Saul and Humphrey 1990; Sestokas and Lehmkuhle 1986; So and Shapley 1979; Troy and Lennie 1987; Yeh et al. 2003). However, the differences in response latencies between X and Y geniculate cells are not clear-cut and latency range within each cell type is very large (about 25 ms) (Troy and Lennie 1987). And even neighboring X geniculate cells that were simultaneously recorded have slightly different response properties, including receptive field positions, receptive field sizes and response latencies. According to our results, even neighboring geniculate cells that were simultaneously recorded showed great variation in receptive field size and response latency. In this aim we investigated whether this variability in response properties is totally random or whether there is a correlation across properties.

To pursue this aim, we introduced a multielectrode array into the LGN of the anesthetized cat and measured response properties of multiple neighboring geniculate

neurons simultaneously recorded (see Methods in Appendix I for details). The receptive fields were mapped by white noise with reverse correlation analysis. The binary 'dense' white noise consisted of an m-sequence of checkerboards of 16X16 pixels (0.9-0.45 deg), each checkerboard being presented for 15.5 ms (Reid et al. 1997; Sutter 1987).

Our results suggest that the receptive field size and response latency of neighboring geniculate cells are correlated: the larger the receptive field, the faster response to visual stimuli (Appendices I & IV). Such inverse relationship between receptive field size and response latency could play an important role in organizing the activity patterns of ensembles of neurons and in generating spatiotemporal dynamics in the visual cortex. A number of behavioral and physiological studies suggest that coarse spatial features are processed before fine details in the visual cortex (Bredfeldt and Ringach 2002; Breitmeyer 1975; Frazor et al. 2004; Harwerth and Levi 1978; Mazer et al. 2002; McSorley and Findlay 1999; Menz and Freeman 2003; Morrison and Schyns 2001; Nishimoto et al. 2005; Pack and Born 2001; Ringach et al. 1997). For example, it has been shown that the peak of spatial frequency tuning of a cortical cell shifts toward higher frequencies as the response progresses in time (Bredfeldt and Ringach 2002; Frazor et al. 2004; Mazer et al. 2002; Nishimoto et al. 2005). Our results strongly suggest that these shifts in spatial frequency tuning arise from differences in the response time course of the thalamic inputs (Frazor et al. 2004; Weng et al. 2005), an idea that has been recently supported by other studies (Allen and Freeman 2006).

A possible mechanism for this space-time correlation is that both receptive field size and response latency depend on the responsivity (i.e. firing rate) of the geniculate cell. That is, cells with the highest firing rates will tend to have the largest receptive field

sizes and fastest response latencies. To test this possibility, we selected 10 groups of simultaneously recorded geniculate cells (> 4 cells per group) that showed strong space-time correlations (r > 0.92) and estimated the contribution of firing rate to these correlations. We found that firing rate was significantly correlated with both receptive field size (r = 0.197, p < 0.05) and response latency (r = -0.203, p < 0.05), however, the correlations with firing rate were too weak to explain the very strong space-time correlations that we found (r > 0.92). To estimate the respective contributions from receptive field size and firing rate to response latency we used multiple regression analysis based on the following model (y = $b_1 x_1 + b_2 x_2$ + error). In this model, $x_1$ is the receptive filed size, $x_2$ is the firing rate and $b_1$, $b_2$, error are free parameters that are adjusted to match as close as possible the measured response latency (y). The results from multiple regression analysis revealed a highly significant contribution of receptive field size to response latency (average $b_1$ = -0.94), but the contribution from firing rate was neglectable and not significant.


**Aim 2. Influence of contrast on the spatial properties of LGN cells (Appendix II)**

Most response properties are stimulus dependent at nearly all stages of visual processing. For example, the response latency of retinal and thalamic neurons changes with stimulus contrast (Benardete et al. 1992; Kremers et al. 2001; Lee 1996; Shapley and Victor 1978) and, at the cortical level, increasing the contrast reduces cortical receptive field sizes by 50-75% and broadens the spatial frequency bandwidth by about 24% (Cavanaugh et al. 2002; Kapadia et al. 1999; Sceniak et al. 2002; Sceniak et al. 1999). Since luminance

contrast is such a fundamental parameter in vision, we want to measure how the response properties shared by neighboring neurons change with stimulus contrast.

To pursue this aim, we recorded simultaneously from multiple LGN neurons with overlapping receptive fields and measured their spatial frequencies at different contrasts. The spatial frequency tuning was measured with gratings drifting at 10 different spatial frequencies (0.07-4.44 c/d) at 2 Hz. The mean firing rates were measured and then fitted with Gaussian functions to calculate the spatial frequency peaks and bandwidths.

Increasing the contrast not only broadened the spatial frequency tuning of the individual cells, but also caused shifts in their optimal spatial frequencies that could be either towards lower or higher frequencies (peak shifts). Interestingly, these peak shifts were not random but depended on the optimal spatial frequency of the cell: cells with low optimal spatial frequencies (< 0.4 c/d) shifted their peaks towards lower frequencies and those with high optimal spatial frequencies (> 0.5 c/d) shifted towards higher frequencies (Appendix II). The value of peak shift was significantly correlated with the optimal spatial frequency of the cell measured at high contrast in our data and similar unreported correlations were found when we re-analyzed the thalamic and cortical data from previous studies (Nolt et al. 2004; Sceniak et al. 2002). Our results indicate that increasing the contrast has a major effect on the spatial frequency tuning of cell populations within LGN and that this population tuning is broadened by two different mechanisms: tuning-broadening of single-cell spatial-frequency bandwidth and tuning-stretching of the cell-population bandwidth, the latter one caused by peak shifts in opposite directions of the spatial frequency spectrum.

**Aim 3. Response properties shared by geniculate afferents that converge at the same cortical domain within primary visual cortex (Appendix III)**

The primary visual cortex is organized in domains of neurons that share similar response properties such as orientation preference, retinotopy and eye dominance. In this aim we investigated the functional micro-organization of the multiple geniculate afferents that converge at the same cortical domain (cortical domain is defined here as a cylinder of 150 μm radius). While there have been very detailed measurements of receptive field scatter for neighboring cortical neurons (Blasdel and Campbell 2001; Bosking et al. 2002; Buzas et al. 2003; Das and Gilbert 1997; Hubel and Wiesel 1974; Yu et al. 2005), the equivalent measurements for geniculate afferents were missing. This is a crucial piece of information that is needed to understand how cortical maps are organized and the role of the different neural connections in cortical mapping. Therefore, we investigated the amount of scatter in receptive field position from convergent geniculate afferents and the functional arrangement of other response properties from geniculate afferents including receptive field sign (i.e. on-center versus off-center).

To pursue this aim, we introduced a silicon probe with 16 different electrodes within the cortex and an array of 7 independently moveable electrodes in LGN to record simultaneously from multiple geniculate cells (single units) and cortical cells (multiunit and LFP), all in precise retinotopic alignment. We used recently developed methods that combine spike trigger averaging and current source density analysis to measure the monosynaptic currents generated by single thalamocortical afferents through the depth of the cortex (Swadlow and Gusev 2000; Swadlow et al. 2002).

Previous studies indicate that the receptive field scatter of convergent geniculate afferents within the cortex is several times larger than the average receptive field size of a layer 4 cortical neuron (Chapman et al. 1991). According to these studies, neighboring geniculate afferents within the cortex can have receptive fields separated in visual space by 12 geniculate centers (Chapman et al. 1991). In contrast, measurements in ferret (Usrey et al. 2003), cat (Alonso et al. 2001; Bullier et al. 1982; Martinez et al. 2005; Priebe et al. 2004) and primate (Ringach et al. 2002) consistently indicate that the average receptive field size of a layer 4 simple cell is 2.5 geniculate centers (1 geniculate center matches the width of each simple cell subregion). Using the new exciting technique of spike-triggered current source density (STCSD) (Swadlow and Gusev 2000; Swadlow et al. 2002), we were able to provide the most accurate measurements of receptive field scatter of convergent geniculate afferents available to date. We solved the above paradox by showing that this amount of receptive field scatter is more restricted than previously thought (Chapman et al. 1991). Remarkably, our findings indicate that the average scatter is 2.5 geniculate centers, which matches nicely with the average receptive field size of a simple receptive field in layer 4 (Alonso et al. 2001; Bullier et al. 1982; Martinez et al. 2005; Priebe et al. 2004).

Our results also indicate that geniculate afferents are sorted within the cortex not only by retinotopy and eye dominance but also by other response properties, for example, receptive field sign (on-center versus off-center) (Appendix III). Here we demonstrate that on- and off-center geniculate afferents segregate in different domains of the cat primary visual cortex and that off-responses dominate the cortical representation of the area centralis. On average, 70% of the geniculate afferents converging at the same

cortical domain had receptive fields of the same contrast polarity. Our results support several computational models that consider the segregation of on- and off-center geniculate afferents as a general feature of cortical functional organization including orientation maps (Miller 1992, 1994; Nakagama et al. 2000; Ringach 2004, 2007).

**Aim 4. Dynamic encoding of LGN cells under natural stimulation (Appendices V-VII)**

The major goal of vision research is to understand how information about the outside world is encoded in the neuronal activity in the visual system. Traditionally scientists presented the animal with basic shapes such as lines, dots and gratings and then studied the resulting pattern of electrical activity in the brain. However, these basic shapes are not what we see every day. Many scientists become increasingly interested to understand how the brain processes natural scenes. With collaboration with Dr. Stanley's lab in Harvard University, we studied neural coding in the cat LGN under natural visual stimulation, combined with traditional stimuli.

To pursue this aim, we recorded simultaneously from multiple LGN neurons with overlapping receptive fields and measured their response properties under different stimuli including white noise stimuli and natural scene movies. The movie was made by a group in Germany using a CCD camera mounted on the head of a freely roaming cat as it made its way through the forest (Kayser et al. 2003).

Sensory neurons can respond extremely precise to repeated stimuli and this precision can be down to milliseconds. However, the relevant timescales of natural vision are much slower. We demonstrate that the relevant timescale of neuronal spike trains

depends on the frequency content of the visual stimulus. And we also show that relative precision is maintained both during spatially uniform white noise stimuli and nature scene movies, which is necessary to represent accurately the more slowly changing visual world (Appendix V). Moreover, we also characterize the adaptation of LGN neurons to changes in stimulus contrast and correlations. We have shown that an increase in contrast or correlations results in receptive fields with faster temporal dynamics and stronger antagonistic surrounds, as well as decrease in gain and selectivity (Appendix VI). We also demonstrate that burst responses in geniculate neurons play a dynamic role during visual processing that may change according to behavioral state (Appendix VII).

# QUESTIONS FROM COMMITTEE

## 1. Questions from Dr. Lee

**Question:**

Elucidate what is meant by a "faster response to a visual stimulus" and describe the mechanisms which make up response latency.

**Answer:**

Response latency is the amount of time taken for a cell to respond to a stimulus. After a visual stimulus is presented, light enters the eye and photoreceptors absorb the photons and transmit signals to bipolar cells, which in turn synapse onto retinal ganglion cells that transmit the sensory information to the rest of the brain. The retinal ganglion cells send visual information in the form of action potentials to the LGN. The time taken for the sensory stimulus to generate action potentials in an LGN cell is called the response latency of the LGN cell.

We have demonstrated that X and Y neighboring cells within the main layers of cat LGN follow a general principle: the larger the receptive field size, the faster the response to the visual stimuli. Therefore, it is noteworthy to discuss the mechanisms that are involved in generating the response latency and receptive field size. An interesting possibility is that both properties depend on the number of convergent inputs that a cell receives (from the photoreceptor to the LGN). Increasing the number of convergent inputs should make geniculate receptive fields larger (more cones per geniculate cell) and visual response faster [more synapses being simultaneously activated lead to a larger compound synaptic potential that reaches threshold faster (e.g., Andreasen and Lambert 1998)]. Data on X

and Y geniculate cells provide support for this 'convergence hypothesis'. Y geniculate cells have larger receptive fields than X geniculate cells because they receive input from more cones (see Sterling 2004 for review), and possibly from more retinal ganglion cells (Yeh et al. 2003). In addition, Y geniculate cells respond faster to visual stimuli than X cells because they may receive input from larger and more numerous synaptic boutons and may be served by thicker/faster axons (Sterling 2004; Sur et al. 1987).

On the other hand, summing a larger number of inputs also improves the signal to noise ratio and the contrast sensitivity. A low contrast stimulus generate the fastest responses in cells with the highest contrast sensitivity, which usually have the largest receptive fields (Shapley and Victor 1978). Therefore, cells with large receptive fields should generate faster responses than other cells because they have higher contrast gain. This mechanism clearly influences the space-time correlations we reported (particularly when using low contrast stimuli). Although the strength of the correlation does not depend on the stimulus contrast, the range of response latencies is reduced when the contrast increases.

The space-time correlations could also be a consequence of a common developmental mechanism of receptive field size and response latency. Just before eye opening, a geniculate cell receives weak synaptic contacts from many retinal ganglion cells, however, as the LGN matures most of the multiple inputs are eliminated (Chen and Regehr 2000; Mason 1982; Sretavan and Shatz 1986; Sur et al. 1984). The elimination of multiple retinal inputs could lead both to a reduction in receptive field size and a faster

synaptic integration (because the remaining inputs become much stronger and therefore reach threshold faster).

**Question:**

What is the relationship between an impulse response and a temporal MTF?

**Answer:**

Both impulse response and the temporal modulation transfer function (TMTF) are used to characterize temporal vision. Dr. Lee and his colleagues compared the impulse response with the TMTF of macaque ganglion cells (Lee et al. 1994). They measured the responses of cells to brief luminance and chromatic pulses and to luminance or chromatic sinusoidal modulations. For the impulse response (IR) function, responses to pulses of opposite polarity were combined to yield a linearized impulse response to make both positive and negative lobes of the pulse response visible. IR was represented as the time course of the response [Note that in our study, impulse response is defined as the time course of the response evoked by the most effective stimulus pixel within the receptive field center and the visual stimulus was white noise checkerboards (Weng et al. 2005)]. For the TMTF, responses at each temporal frequency were averaged for a range of contrasts and first-harmonic response amplitudes were then extracted by Fourier analysis of response histograms to calculate responsivity (imp / sec / % contrast). TMTF was represented as a responsivity function of temporal frequency.

TMTF can be used to derive impulse-response functions, either by assuming some sort of filter model or by numerical methods (Lee et al. 1990; Stork and Falk 1987; Swanson et

al. 1987). Lee et al found that for ganglion cells of the parvocellular (PC) pathway, shape and absolute amplitude of linearized pulse responses corresponded well to the predicted responses over a range of pulse durations for both luminance and chromatic modulation. For ganglion cells of the magnocellular (MC) pathway, shape and amplitude of the linearized pulse responses and the predicted responses corresponded well when the product of pulse duration and contrast was low, but less well predicted for long duration-high contrast stimuli.

**Question:**

Describe some reasons why response latency should decrease as contrast increases - I can think of 4 somewhat interrelated reasons.

**Answer:**

1. Contrast gain control

Shapley and Victor demonstrated a phase-advance at the level of the retinal ganglion cells with increasing contrast and proposed that this advance was a consequence of a contrast gain control mechanism (Shapley and Victor 1978). The contrast gain control model can be described as an increase of high temporal frequency responses relative to low temporal frequency responses as contrast increases. The classical center-surround receptive field of a ganglion cell constitutes an approximate linear filter, that I call L. L receives direct input, $I_D$, and its response varies sinusoidally with the spatial phase of the stimulus. For a linear system, the response amplitude should grow proportionally with the stimulus contrast and the phases of the responses should remain the same. However, in fact, as contrast increases, the responses of ganglion cells at the high frequencies are

enhanced relative to the responses at low frequencies, which suggests that some functions of the over-all power in the stimulus modifies the liner transfer properties of retinal ganglion cells. One would expect that power at different temporal frequencies should have different degrees of influence on the linear transfer properties. Therefore, it has been suggested that L also receives another input, $I_C$, which is produced by the contrast gain control C. The hypothesis is that C measures the contrast of the stimulus at many separated points in the visual field over a region at least as large as the conventional center and surround. In this way, the signal $I_C$ can be independent of the spatial phase of a grating stimulus. Since increasing contrast increases the responses at high frequencies more than those at low frequencies, the effect of contrast may be to decrease the number of effective low pass stages in L. The more enhanced responses at the high frequencies relative to the low frequencies generate a rightward shift in the temporal frequency tuning curve. And this would produce a phase advance at frequencies above the corner frequency of the low pass filters involved.

2. Changes in baseline membrane potential

Intracellular studies of retinal ganglion cells have shown contrast-dependent changes in the baseline membrane potential (Baccus and Meister 2002; Zaghloul et al. 2007). Increasing stimulus contrast causes a depolarizing shift in the baseline membrane potential, enabling the cell to generate action potentials faster.

3. Changes in the number of inputs

When the stimulus contrast is increased more photoreceptors could be activated. As a result, more retinogeniculate synapses will be activated, which may lead to a larger compound synaptic potential that reaches threshold faster.


4. Center-surround antagonism

We have shown that the surround/center ratio of LGN receptive fields increases with contrast (Lesica et al. 2007). The strengthening of the surround relative to the center may contribute to a decrease in the overall response gain of the cell and generate a phase advance as predicted by the contrast gain control model.


**2. Questions from Dr. Zaidi**

**Question:**

What are the assumptions that a cell must satisfy for the reverse correlation technique to give valid results?  How would you test these assumptions independently for an LGN neuron?

Answer:

We used the white noise stimulus with reverse correlation to map the receptive fields of LGN cells. The stimulus contained thousands of frames of checkerboards with white and black squares. We averaged the stimulus frames that preceded an LGN spike with a certain time delay.  The reverse correlation method makes the assumption that cells respond linearly. That is, the response to the sum of two stimuli is equal to the sum of the responses to two individual stimuli. Therefore, reverse correlation delivers accurate

spatial and temporal estimates of the linear component of a receptive field but it does not take into account possible non-linearities (Reid et al. 1997). For example, this method provides a relatively complete description of the spatiotemporal structure of an X cell's linear receptive field but it does not reveal the nonlinear receptive field subunits of Y receptive fields. That being said, the receptive fields measured with the reverse correlation technique can be used to accurately predict LGN responses at the millisecond scale (Butts et al. 2007).

Another assumption that we make when we use the reverse correlation technique is that the size of each white-noise pixel is several times smaller than the receptive field center of the LGN cell. To fulfill this assumption in our experiments we adjusted the size of each pixel to be at least 1/3 the geniculate center size.

**Question:**

What does it mean that a white noise image is uncorrelated but a natural image is not? How would you measure correlations in a natural image? What is "neural decorrelation"? How is it related to "redundancy reduction"? Do you have any evidence in your papers of adaptation to spatial correlations leading to decorrelation or redundancy reduction?

**Answer:**

1. Our white noise stimuli are made of checkerboards with white and black squares that change pseudo-randomly over space or time (the randomization is determined by an m-sequence). Because of the randomization, there are no spatiotemporal correlations in the white noise. For example, neighboring black-white pixels are found with the same

probability as neighboring black-black or neighboring white-white pixels (this is true both in space and time).

Natural scenes are very different from white noise in their spatiotemporal correlations. The individual pixels in natural scenes are highly correlated in both space and time. For example, the pixels in a white cloud are highly correlated in space (the probability of finding neighboring white-white pixels is much higher than the probability of finding neighboring white-black pixels). Also, the pixels in a white cloud are highly correlated over time (if we take a movie of the white cloud, white pixels will be followed by white pixels over long periods of time). In general, light intensities at neighboring locations and times tend to be very similar, except at edges (Dong and Atick 1995).

2. The spatiotemporal correlations of a natural image can be measured by calculating the power spectrum in both spatial and temporal domains. For example, at a certain temporal frequency, we can conduct a Fourier transform of the different spatial frequencies. For the natural image, there would be more power at low frequencies and the power would decrease with increasing frequencies in both spatial and temporal domains. For the white noise stimulus, we would obtain a flat power spectrum in both spatial and temporal domains because the white noise stimulus has the same energy at all frequencies (Lesica and Stanley 2004).

3. Decorrelation is a general term for any process that is used to reduce autocorrelation within a signal, or cross-correlation within a set of signals, while preserving other aspects

of the signal. Neural decorrelation is a strategy used by neurons to remove redundant information in the sensory input data, i.e. 'redundancy reduction'.

4. We have shown that changes in stimulus parameters (contrast or correlation) not only affect the response latency, but also affect the interactions between receptive field center and surround. When we compared the responses during stimulation with natural scene movies and white noise, we found that receptive field surround became substantially weaker at white noise stimulation than at natural scene stimulation. Since natural stimuli contain strong spatial correlations, the increased strength of the receptive field surround during natural stimulation decreases sensitivity of the neuron to these correlations (Lesica et al. 2007).

### 3. Questions from Dr. Swadlow

**Question:**

Review the non-retinal inputs to the LGNd and compare them to the retinal inputs.

With specific reference to the thalamic reticular nucleus (it is called something else in the cat), what is known about the inhibitory inputs to LGNd neurons from these cells. What are the receptive field properties of the TRN cells? Do they receive input from both X and Y cells, and do they project selectively or non-selectively to X and Y cells?   (i.e., is the feedback inhibition "broadband" or selective?)

Now, for the real question:  How might this inhibitory input have influenced your tuning curves under low vs. high contrast?

**Answer:**

1. LGNd is a thalamic nucleus that receives its main inputs from retina, visual cortex, brain stem and thalamic reticular nucleus (TRN). The visual part of the TRN is called the perigeniculate nucleus (PGN). The direct inputs from retina, brainstem and visual cortex are all excitatory. The retina provides around 10% of the excitatory synapses on the LGN. The visual cortex and brain stem provides the rest of the excitatory synapses in approximately equal proportions. The inhibition within LGN is provided by the inhibitory neurons of the TRN and interneurons within LGN itself. Inhibitory inputs makes about 25% of all the synapses within LGN (for review, see Derrington 2001).

2. TRN has a shell-like structure surrounding most parts of the dorsal thalamus. Because of this anatomical location, virtually all axons passing between dorsal thalamus and cortex must go through TRN. Many of the geniculocortical and corticogeniculate axons innervate the TRN cells, with glutamatergic afferents that are generally excitatory (Sherman and Guillery 2001). TRN cells provide inhibitory feedback input to LGNd relay neurons by releasing neurotransmitter γ–aminobutyric acid (GABA) (Jones 1985; Ohara and Lieberman 1985; Sanchez-Vives and McCormick 1997). It has been suggested that these inhibitory effects include recurrent inhibition, lateral inhibition, long-range inhibition, and binocular inhibition (Dubin and Cleland 1977; Eysel et al. 1986; Guido et al. 1989; So and Shapley 1981; Xue et al. 1988).

3. Receptive field properties of the TRN cells:

- TRN cells have large and diffuse receptive fields (Funke and Eysel 1998; Sanderson 1971; Uhlrich et al. 1991; Wrobel 1981; Wrobel and Bekisz 1994), roughly twice as large as LGN cells at the same eccentricity (Wrobel 1981);

- TRN cells exhibit mixed on-off response with responding equally to light increments and decrements (Dubin and Cleland 1977; Funke and Eysel 1998; Sanderson 1971; So and Shapley 1981; Uhlrich et al. 1991; Wrobel and Bekisz 1994; Xue et al. 1988);

- TRN cells are generally binocularly innervated (Dubin and Cleland 1977).

4. X and Y cells seem to activate separate categories of TRN cells (Ahlsen et al. 1983; see also Dubin and Cleland 1977; Wrobel and Bekisz 1994).

5. The inhibitory input from TRN may play a role in sharpening the spatial frequency tuning curves of LGN cells. Increasing contrast might increase the inhibition and sharpen the tuning curves. However, we found that the tuning curves become broader at high contrast than at low contrast. One possibility is that this inhibitory input from TRN may have a very subtle effect on the spatial frequency tuning curves of LGN cells. Another possible mechanism is that this inhibitory effect gets saturated at high contrast and therefore the sharpening effect may be similar at different contrasts.

**Question:**

A temporal frequency of 2 Hz nearer to the optimal frequency for high spatial frequency cells, which tend to be X, than to low spatial frequency cells. If so, how might this have influenced your data, and how would you control for this?

**Answer:**

Both X and Y cells have low-pass temporal frequency tunings, which have the highest sensitivity at low temporal frequencies and the sensitivity systematically decreases at higher temporal frequencies. Y cells tend to exhibit more sensitivity to higher temporal frequencies and have higher cut-off temporal frequencies than X cells. At the low temporal frequencies (1-4Hz), both X and Y cells exhibit maximum responses (Lehmkuhle et al. 1980). Therefore, our stimulus with temporal frequency at 2 Hz is unlikely to influence our measurements of spatial frequency tuning curves at different contrasts.

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**APPENDICES: ORIGINAL PUBLICATIONS**

# APPENDIX I


## Receptive field size and response latency are

## correlated within the cat visual thalamus

Weng C, Yeh CI, Stoelzel CR, and Alonso JM

# APPENDIX II


**Influence of contrast on the spatial frequency tuning of**

**neuronal populations in the cat visu al thalamus**

Weng C, Jin JZ, Yeh CI, and Alonso JM

In preparation.

# APPENDIX III

## On- and off-domains of geniculate afferents

## in cat primary visual cortex

Jin JZ, <u>Weng C</u>, Yeh CI, Gordon JA, Ruthazer ES,

Stryker MP, Swadlow HA and Alonso JM

# APPENDIX IV

## Retinogeniculate connections: a balancing act between connection specificity and receptive field diversity

Alonso JM, Yeh CI, <u>Weng C</u>, and Stoelzel CR

# APPENDIX V


## Temporal precision in the neural code

## and the timescales of natural vision

Butts DA, <u>Weng C</u>, Jin JZ, Yeh CI, Lesica NA, Alonso JM, and Stanley GB

Nature, 449: 92-95, 2007.

# APPENDIX VI

## Adaptation to stimulus contrast and correlations

## during natural visual stimulation

Lesica NA, Jin J, Weng C, Yeh CI, Butts DA, Stanley GB, and Alonso JM

# APPENDIX VII

## Dynamic Encoding of Natural Luminance

## Sequences by LGN Bursts

Lesica NA, <u>Weng C</u>, Jin J, Yeh CI, Alonso JM, and Stanley GB